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has come to the conclusion that Grüneisen's theory can not be more than a first approximation. This conclusion will not be altered by using the values of the table above instead of those of Beckman.

The theory of Grüneisen is incomplete in the sense that it gives the pressure coefficient of resistance in terms of the temperature coefficient as well as several thermodynamic constants. I hope to show at some length elsewhere that both the temperature and the pressure coefficient of resistance may be calculated with better agreement than by Grüneisen's formula by putting the proportional change of resistance in any direction equal to twice the proportional change of average amplitude of atomic vibration. This is capable of theoretical explanation on the ground that when the atoms are at rest the electrons pass freely from atom to atom, but when the separation of the atoms by haphazard heat agitation becomes too great, the electrons encounter difficulty in jumping from atom to atom.

The expenses of this investigation were in large part met by generous appropriations from the Bache Fund of the National Academy of Sciences, and from the Rumford Fund of the American Academy of Arts and Sciences.

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[1] Lisell, E., Inaug. Dis., Upsala, 1902; and Beckman, B., Inaug. Dis., Upsala, 1911; *Ark. Mat. Astr. Fys.*, 7, 1912, No. 42 (1–18); *Ann. Physik., Leipzig*, **46**, 1915, (481–502) and (931–941); *Physik. Zs., Leipzig*, **16**, 1915, (59–63).

[2] Grüneisen, E., *Berlin, Verh. D. physik. Ges.*, **15**, 1913, (186–200).

THE RATE OF DISCHARGE OF CENTRAL NEURONES

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Communicated by W. B. Cannon, November 27, 1916

The frequency of nerve impulses discharged from the central nervous system in voluntary and reflex contraction of the skeletal muscles presents a problem concerning which great difference of opinion is found among investigators. Piper, studying the electrical disturbance with a string galvanometer, has shown that in human muscles a fairly regular series of action currents with a rhythm of about 50 per second accompanies voluntary contraction. He inferred from this that the central nervous system sends to the muscle 50 impulses per second.

Buchanan, chiefly on the basis of experiments on frogs, reached the conclusion that the observed rhythm is not that of the motor nerve impulses but is dependent on the condition of the muscle itself.

By applying the principle of Buchanan's experiments to human muscles we have obtained results which confirm her main conclusion. Electrodes connected with a string galvanometer were so applied to the skin as to lead off the action currents of the first dorsal interosseous muscle lying close under the skin between the thumb and forefinger. Records were made in this way with the muscle in voluntary contraction at normal, subnormal and supernormal temperatures. Lowering of temperature was produced by immersing the hand and most of the forearm in water as cold as could readily be borne (6° to 7°C)., for about fifteen minutes; heating was produced by immersion in water at 45°C. for a somewhat shorter time. By immersion to a point above the elbow the forearm flexor muscles were treated and investigated in the same way. An unmistakable and fairly marked decrease in the frequency of muscular action currents results from this process of chilling; and an increase, which, as is to be expected, is less marked, results from heating. As nearly as can be judged from the somewhat irregular oscillations, the average action current frequencies at the three temperatures studied were in the case of the interosseous muscle as follows: cold 39 per second, normal 56 per second, hot 63 per second, in the case of the forearm flexors the corresponding estimates are, cold 36, normal 48, hot 50. We claim no strict quantitative accuracy for these figures, but the uniformity of the estimates justifies the conclusion that there is a real change of rhythm correlated with change of temperature. The temperature of the body as a whole was shown to undergo no significant change during the experiments.

The result apparently leads to the conclusion that the observed electrical muscle rhythm is not that of central innervation. It is difficult to conceive how a change in temperature in the muscle could alter the frequency of discharge of impulses from the ganglion cells whose temperature remains constant. But each propagated disturbance in a muscle fiber must depend on stimulation by a nerve impulse. Nerve impulses must therefore be so distributed in time as to render possible various frequencies of response such as those observed, depending on the temperature of the muscle. This demands a higher frequency of nerve impulses than that observed in the muscle rhythm. A careful study of the most perfectly rhythmical oscillations in our records leads us to estimate that there must be at least 300 nerve impulses per second to account for the muscle rhythms shown to be possible at various temperatures.

Piper's strongest argument against Buchanan's view of muscle rhythm which we here substantiate, is that the frequency of stimuli applied to a motor nerve can be raised as high as 300 per second and a corresponding action current rhythm will still appear in the innervated muscle. If the muscle can respond separately to as many as 300 nerve impulses per second, he argues that it will not respond as slowly as fifty times per second unless it is stimulated only fifty times per second.

An explanation of the paradox is found in an analysis of the series of events involved in the excitation of a muscle through its nerve, in the light of certain functional properties shown by Lucas and Adrian to be essentially common to the two tissues. In either tissue a response is followed by a brief 'refractory period,' at first absolute when the tissue cannot be excited, then relative when the tissue can only be excited by a stronger stimulus than usual, and when the response is of subnormal magnitude. During the relative refractory period the excitability and the magnitude of response both return gradually to normal. At all times, including the refractory period, the magnitude of response in nerve is independent of the strength of stimulus and dependent only on the state of the tissue. The refractory period in nerve, though similar to that in muscle is much shorter.

If we assume that the stimulating effect of the nerve impulse on muscle is correlated with its magnitude as shown by other criteria, then we find no conflict between the ability of muscle to respond separately to 300 impulses per second and its response at a slower frequency to nerve impulses of a higher frequency. For as each nerve impulse is made to come earlier in the nerve's refractory period which was due to the preceding impulse, its magnitude is reduced till, coming at so early a stage in the refractory period of the muscle, it fails to excite it. One or more nerve impulses will be ineffective following each that is effective. The higher the nerve frequency the weaker will be each impulse and the more must the muscle recover to be again excited. Thus after the critical frequency is reached, the higher the nerve frequency the slower the muscle rhythm. In this respect we depart from Buchanan's view to the extent of supposing an indirect dependence of muscle rhythm upon nerve rhythm.

In view of this analysis, since the nerve rhythm evidently does not correspond with the muscle rhythm, it must have a higher frequency than the critical value (300 or more per second) below which the muscle can follow the nerve rhythm; otherwise the muscle rhythm would correspond with it.

Inferences based on these considerations together with observations of Lucas, Adrian and Garten, lead us to suppose that the normal frequency of nerve impulses discharged from the ganglion cells in voluntary contraction must lie between 300 and 5000 per second.

The complete paper will appear in the *American Journal of Physiology*, January, 1917.

A PHYSIOLOGICAL STUDY OF NOCTILUCA, WITH SPECIAL REFERENCE TO LIGHT PRODUCTION, ANAESTHESIA AND SPECIFIC GRAVITY

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Communicated by A. G. Mayer, December 5, 1916

The specific gravity of *Noctiluca* is less than that of sea water, so that normally the animals float at the surface. They contain no air bubbles or large oil drops, and their lower specific gravity must therefore be due to a lower salt content than the sea water. In more concentrated sea water, the animals shrink and in more dilute sea water they swell; the plasma membrane therefore has the usual semipermeability toward the balanced salts of sea water, i.e., permeability to water and impermeability to salts. When placed in a mixture of 4 sea water; 6 fresh water, the animals sink, their salt content being now greater than that of the surrounding medium, but later they rise to the surface, a process independent of the movement of the tentacle. They must therefore have absorbed water not only until their salt content is the same as that of the surrounding medium (when they should still sink), but enough water to make their salt content again less than the 4 s.w.: 6 f.w. mixture, thus re-establishing their normal relation to the surrounding medium. This water must be absorbed against the osmotic pressure of the salts of sea water, a process contrary to physical laws. The animals can not only lessen their specific gravity, but they can also increase it, as is shown by the fact that on windy days they sink far beneath the surface of the sea. Anesthetics, acids and alkalies, KCN, and the pure solutions of the salts of sea water do not interfere with this regulatory mechanism except when they cause irreversible changes and death of the cells; dead *Noctiluca* always sinks to the bottom.

Light production in *Noctiluca* normally occurs only on stimulation of any kind, and is a momentary bright flash; dying animals produce a bright steady glow. The luminescence is traceable to points of light coming from granules in the protoplasm. No substances were found which would cause a rhythmic flashing, comparable to the rhythmic